The phylogenetic development of food selection in certain Orthopteroids

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The horse, *Equus,* has long enjoyed a kind of pre-eminence in the eyes of biologists. So instructive and apparently well-documented are the facts of its evolution that a discussion of them is a part of most elementary courses in zoology. Several decades of students have been taught that the horse finds its origin in the Eocene with the rise of the humble forest-dweller *Eohippus.* This cat-sized animal of browzing habit was dramatically transformed into modern *Equus* through a series of increases in body size and changes in teeth and legs adapting it for a cursorial, grazing existence. These adaptations followed known changes in the Tertiary landscape from moist woodland to dry grassland.

Few appreciate that parallel correlations are obtainable from among the insects. The fact that they are was forcibly drawn to my attention when recently, in connection with another investigation, I perused the literature of paleoentomology. The phylogenetic conclusions and geologic ranges discussed by Zeuner and others, viewed in light of food selection in extant orthopteroids, disclosed certain recognizable patterns reminiscent of those seen in horse evolution. These patterns are the subject of this article. Its content is both controversial and speculative. It assumes that one can deduce the habits of organisms of the past on the basis of their structural adaptations, seen in light of behavior in modern species. It also presupposes a rather precise knowledge of the geologic range of the major plant and insect groups and of food selection in the orthopteroids in question. Unfortunately no such body of information —one sufficiently extensive and reliable to permit unquestioned generalization— exists. Nevertheless, the patterns are there, and, however tentative, seem worth description and interpretation.

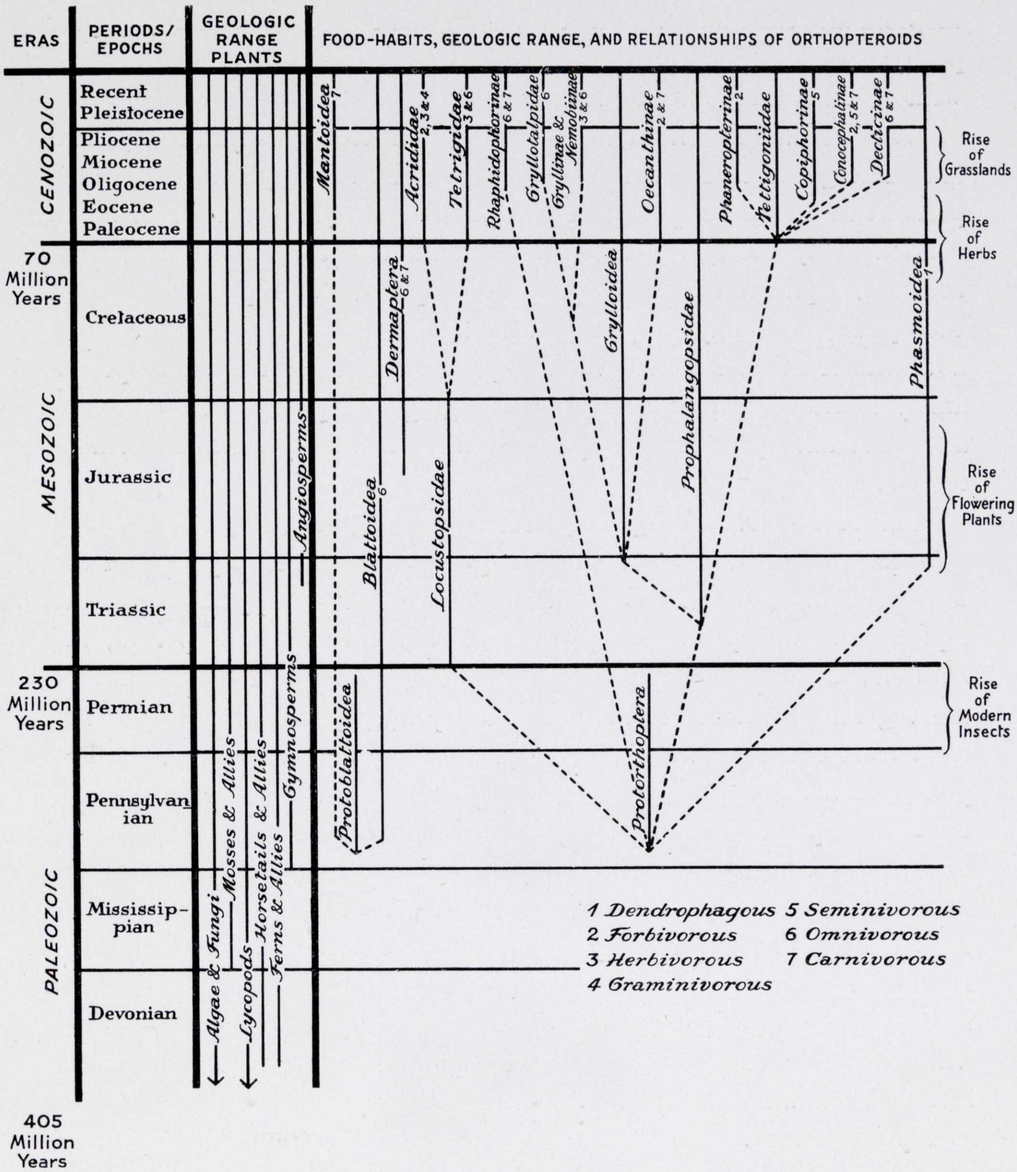
The Pennsylvanian. Our story begins in the Pennsylvanian, a

period of moist, equable climate when luxuriant swamps were more extensive than at any other time in the earth's history. Little is known about conditions in the uplands, but in the lowlands marshes and sheets of water interspersed with low hills reached to the horizon. These situations supported a varied fauna and flora of ancient types (Table I, II). The insects of the time included, among others, the protoblattoidean and protorthopteran groups (both now extinct), the extant cockroach (blattoidean) group, and perhaps even some ensiferous grasshoppers. They shared the terrestrial environment with various other insects *(viz.,* the extinct groups Megasecoptera, Protephemerida, Protohemiptera, and especially the Paleodictyoptera and Protodonata) and other arthropods (arachnoids, centipedes, millipedes), as well as with snails and amphibians. They occurred in a plant setting that included algae, fungi, mosses, liverworts, ferns; herbaceous and arborescent seed ferns, horsetails, club mosses; and arborescent conifers and cycads.

The ancestral cockroaches are particularly abundant in the Pennsylvanian fossil record. Many of the fossil species were remarkably similar to the cockroaches of today; according to the American paleoentomologist Carpenter, they differ chiefly in wing venation, though one important group (the archimylacrids) was unusual in possession of a long, prominent ovipositor. On the basis of this apparent similarity in appearance and adaptation, and of our understanding in modern species, I think it likely that the Pennsylvanian cockroaches were omnivorous, selecting widely from both plant and animal materials. They perhaps ate a preponderance of plant substances, taken either dead or alive, and supplemented this diet with the dead bodies of other arthropods and even amphibians. This view of food selection is consistent with the occurrence of the Pennsylvanian species; their most abundant remains are associated with the kind of accumulations of plant debris that produced coal beds.

Feeding among the protoblattoideans and protorthopterans can only be surmised. The general body form of the protoblattoideans suggests that they, like the cockroaches, might have been omnivorous. The protorthopterans appear more specialized, and, according to Carpenter, present highly diversified adaptations for feeding. Some must have been outright vegetarians. Others, characterized by raptorial fore legs, were clearly predacious. They probably ate awkward, slow-moving paleodictyopterans as well as other archaic insect types.

TABLE I.



EXPLANATION OF TABLE I.

The food-habits, geologic range, and probable phylogeny of certain orthopteroids is given in relation to the geologic time scale and the geologic range of selected plant groups. The food-habits are based on Gangwere (1961); the phylogeny of Orthoptera on Zeuner (1939, 1941); and the geologic range of both plants and Orthoptera are based on standard works.

In modern times carnivorous and omnivorous habits (both developed by the Pennsylvanian) occur in virtually all major lines of Orthoptera and their allies. The two, along with vegetable feeding (phytophagy), constitute the ancestral patterns inherited by all recent groups, with or without modification.

The Permian. The Permian was characterized by the marked land emergence that ushered in the close of the Paleozoic Era. This period saw the development of an extraordinarily diverse insect fauna dominated by the newly arisen modern insects *(viz.,* Coleoptera, Corrodentia, Ephemerida, Homoptera, Mecoptera, Neuroptera, Odonata, Plecoptera, and Thysanoptera), which shared the scene with various now-extinct orders. The availability of such a diverse fauna presumably made more feasible both scavenging and predatism on insects, and must have prompted adoption of these habits by Permian orthopteroids.

The Mesozoic. The geologic revolution begun during the Permian continued and reached its highest expression in the first period of the Mesozoic, the *Triassic,* when the archaic insects disappeared and the reptiles and dicotyledonous plants arose. In the second period, the *Jurassic,* a mild, moist climate prevailed over much of the earth, and the vegetation differed from that of today largely in that broad-leaved trees were few in number and kind. During the *Cretaceous,* the last period of the Mesozoic, the vegetation of the world was transformed. Flowering plants became conspicuous and then rose to dominance over ferns, conifers, and other gymnosperms. The Cretaceous flora included algae, fungi, mosses, liverworts, ferns, a few cycads, and conifers, together with many dicots and some herbaceous monocots. Among the woody dicots were beeches, birches, cinnamons, elms, figs, magnolias, maples, oaks, sycamores, tulip trees, walnuts, and willows; among the monocots grasses, palms, and sedges. The fauna included mammals and birds, which took their place with the new flora as reptiles waned. Finally the Mesozoic closed, accompanied by great crustal changes and marked modifications of climate.

The Mesozoic (Triassic) appearance of the first walking-sticks (Phasmoidea) was apparently correlated with the rise of woody dicots, a new food source making possible the insects' woody plant foliage feeding (dendrophagy). Certain other orthopteroid groups also differentiated during the Mesozoic. The first prophalangopsids and crickets (Grylloidea) appeared in the Triassic, and somewhat later (in the

Jurassic) came the earwigs (Dermaptera). The evolution of these three groups, unlike that of the walking-sticks, appears *not* closely associated with the rise of dicotyledonous vegetation; they merely followed in the omnivorous-carnivorous tradition.

The Tertiary. The gymnosperms began to wane and the herbaceous monocots and dicots became increasingly prominent in the Tertiary, the first period of the Cenozoic. Large temperate forests of woody dicots developed in lowland areas, and as the monocots and herbaceous dicots continued their ascent were modified in the arid Miocene and Pliocene. Finally the widespread forests of the Upper Cretaceous and early Tertiary gave way to extensive grassland and scrub in the interiors of the continents.

Numerous groups of orthopteroids evolved during this time. Many retained ancient food-habits, but they added at least one innovation: the vegetarians among them now took herbaceous monocot and dicot materials in quantity, and the carnivores supplemented their insect diet with bodies of mammals and birds. The listrosceline and sagine katydids and the mantids were among those orthopteroids that retained a form of carnivory *(viz.,* predatism) as their way of life. The shield-backed katydids (Decticinae), camel crickets (Rhaphidophorinae), field crickets (Gryllinae), ground crickets (Nemobiinae), mole crickets (Gryllotalpidae), and tree crickets (Oecanthinae) also retained the omnivorous-carnivorous mode of feeding; they were either omnivorous, modified omnivorous, or omnivorous-carnivorous. Today —presumably as they were then— they are omnivores exhibiting marked tendencies toward carnivory. Notable among the newly evolved orthopteroids with an ancient mode of feeding are the grouse locusts (Tetrigidae), omnivores which emphasize "lower" plants such as algae in their diet.

The rise of certain other orthopteroids appears to be more closely associated with the further development of monocots and dicots. Though some katydids retained omnivorous or carnivorous tendencies, others adopted various types of plant feeding (phytophagy); the broad-leaved herb feeding (forbivorous) bush and round-headed katydids (Phaneropterinae) and the herb-animal feeding (forbivorous-carnivorous) meadow katydids (Conocephalinae) are examples. They arose during the Tertiary, presumably in response to the development of herbaceous monocots and dicots. Perhaps the origin of katydids is even more specialized. The Russian investigator E. K. Grinfeld

TABLE II.

Summary of Orthopteroid Groups Treated Herein, Their General Food-Habits, and Their Probable Geologic Range.

Group	*Food-Habits*	*Geologic Range*
Protorthoptera	Various including phytophagous (plant feeding) & carnivorous (?)	Pennsylvanian; now extinct
Protoblattoidea	Omnivorous (?)	Pennsylvanian; now extinct
Blattoidea (Cockroaches)	Omnivorous	Pennsylvanian
Phasmoidea (Walking-Sticks)	Dendrophagous (woody plant foliage feeding)	Triassic
Dermaptera (Earwigs)	Omnivorous-carnivorous; omnivorous	Jurassic
Mantoidea (Praying Mantids)	Carnivorous	Tertiary
Acrididae (Grasshoppers)	Graminivorous (grass feeding); forbivorous (broad-leaved herb feeding); or both.	Tertiary
Tetrigidae (Grouse Locusts)	Herbivorous-omnivorous	Tertiary
Rhaphidophorinae (Cave & Camel Crickets)	Omnivorous-carnivorous; omnivorous	Tertiary
Phaneropterinae (Bush & Round-Headed Katydids)	Forbivorous; occasionally dendrophagous	Tertiary
Copiphorinae (Cone-Headed Katydids)	Seminivorous (grass "seed" feeding)	Tertiary
Conocephalinae (Meadow Katydids)	Forbivorous-carnivorous; sometimes seminivorous	Tertiary
Decticinae (Shield-Backed Katydids)	Omnivorous-carnivorous; omnivorous	Tertiary
Gryllinae & Nemobiinae (Field & Ground Crickets, resp.)	Omnivorous-herbivorous	Tertiary
Oecanthinae (Tree Crickets)	Forbivorous-carnivorous; omnivorous.	Tertiary
Gryllotalpidae (Mole Crickets)	Omnivorous; sometimes omnivorous-carnivorous.	Tertiary

(Ent. Obozr., 36, pp. 619-624) has gone so far as to ascribe it to forb pollen feeding.

The rise of at least two other groups, the grass feeding (graminivorous) grasshoppers (Acrididae) and the grass "seed" feeding (seminivorous) cone-headed katydids (Copiphorinae) must have been related directly to the appearance of open land, especially grassland. Grasshoppers, like horses, are characteristically plains and savannah organisms, bound to grasslands both for food and habitation. The first known grasshoppers had already appeared by the Paleocene, but the group apparently did not flourish until the Oligocene and Miocene, when grasslands became widespread.

Discussion.

That correlations exist between the geological appearance of foods and that of their orthopteran feeders is not surprising. A simple comparison of the Paleozoic flora with the Recent one demonstrates the profound differences that can exist between two floras widely separated in time. The plants of the Paleozoic were largely seed ferns, gymnosperms, and "lower" plants; angiosperms (the flowering plants that now dominate the plant world) were completely absent, but when they became available the whole aspect of the flora changed, and a host of new food-feeder relationships became possible.

The several correlations noted above parallel those already seen in other animal groups, and underscore the fundamental nature of food-feeder relationships. The correlations in certain mammals are so well-known as to make unnecessary further discussion of them. Those relative to insects are apparent in several groups but are seldom discussed; among the insects involved are certain wood-dwelling beetles (that arose, together with their food plants, in the Jurassic) and the Lepidoptera and "higher" Diptera and Hymenoptera (that appeared slightly before or during the Tertiary, presumably in association with the burgeoning flowering plants). Future scrutiny of other insect groups should disclose additional patterns of this nature.

Lest the reader be led astray, qualification is required on several points. The events depicted above are a gross oversimplification. New types of food do not arise in splendid isolation, but appear as a result of complex changes within the total environment. It is mislead-

ing to speak, for example, of the onset of grass feeding as a matter aside from the appearance of the open plains and savannah situations that, in the first place, make possible the wide availability of grasses. The rise of new foods is, indeed, only one of numerous factors responsible for the evolution of orthopteroids. The grouse locusts, omnivores with a special attraction to "lower" plants, are one of several groups that testify eloquently to this point; they did not appear until the Tertiary, though their food needs could have been satisfied eons earlier. Their evolution awaited the development of the acridoid ancestral stock from which they radiated. Finally, the conclusion should be dispelled that the Paleozoic and Mesozoic insects were generalized types leading up to more specialized Tertiary and Recent ones. According to Carpenter (personal communication), there is now evidence that the Paleozoic orthopteroids actually showed more structural diversity than do the Recent ones and that they radiated out in many directions, not solely toward the type of later forms.

Summary and Conclusions.

Most food-habits in Orthoptera and their allies are widespread (Table I), occurring in several major phylogenetic lines. One of the first such habits to develop was omnivory, and it was a kind that perhaps emphasized the eating of dead plant and animal materials. It appeared in the cockroaches and presumably also in the protoblattoideans of the Pennsylvanian. In the protorthopterans of the same period there occurred various food-habits including plant feeding and predatism. Thus established, these several ancestral patterns were retained in a number of groups and modified in others as the development of new foods allowed.

The first major departure from the above ancestral patterns occurred in the Triassic, when woody dicots became available as food, making possible the rise of the woody plant foliage feeding walking-sticks. The second major break was in the Miocene and Pliocene, when herbaceous monocots and dicots became abundant and open grasslands (the favorite haunts of many Orthoptera) replaced the widespread forests of earlier times. Several orthopteroid groups appeared and adopted forb (broad-leaved herb) feeding, grass feeding, and related habits; examples are the grasshoppers, bush and round-headed katy-

dids, cone-headed katydids, and meadow katydids. Certain other orthopteroids continued in the omnivorous-carnivorous tradition as they arose, but modified their diet to make use of large quantities of the new plant and animal foods; included are the shield-backed katydids, various true crickets, the camel crickets, and the grouse locusts.

I conclude, therefore, that changes in the availability of foods during geologic time were important factors in the evolution of many orthopteroids; that in other groups they were relatively unimportant; that the food-habits of many Recent orthopteroids are comparatively modern, extending in time only as far as the Tertiary; and that the habits of other groups are exceedingly ancient, taking root in the distant Carboniferous.

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